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Abstract. A map of burn severity resulting from the 1988 fires that occurred in Yellowstone National Park (YNP) was derived from Landsat Thematic Mapper (TM) imagery and used to assess the isolation of burned areas, the heterogeneity that resulted from fires burning under moderate and severe burning conditions, and the relationship between heterogeneity and fire size. The majority of severely burned areas were within close proximity (50 to 200 m) to unburned or lightly burned areas, suggesting that few burned sites are very far from potential sources of propagules for plant reestablishment. Fires that occurred under moderate burning conditions early during the 1988 fire season resulted in a lower proportion of crown fire than fires that occurred under severe burning conditions later in the season. Increased dominance and contagion of burn severity classes and a decrease in the edge: area ratio for later fires indicated a slightly more aggregated burn pattern compared to early fires. The proportion of burned area in different burn severity classes varied as a function of daily fire size. When daily area burned was relatively low, the proportion of burned area in each burn severity class varied widely. When daily burned area exceeded 1250 ha, the burned area contained about 50 % crown fire, 30 % severe surface burn, and 20 % light surface burn. Understanding the effect of fire on landscape heterogeneity is important because the kinds, amounts, and spatial distribution of burned and unburned areas may influence the reestablishment of plant species on burned sites.

Keywords: GIS; Landscape ecology; Landsat Thematic Mapper; Remote sensing; Scale; Spatial heterogeneity.

Abbreviations: GIS = Geographical Information Systems; TM = Landsat Thematic Mapper; YNP = Yellowstone National Park.

Introduction

One of the most striking features of the 1988 fires that occurred in Yellowstone National Park (YNP) was the resulting heterogeneity of the burned landscape and the variable fire severity within burned areas (Christensen et al. 1989). Large-scale crown fires rarely consume an entire forest because of the influence of wind variations, topography, vegetation type, natural fire breaks, and the time of day that the fire passed through (Rowe & Scotter 1973; Wright & Heinselman 1973; Van Wagner 1983). Thus, crown fires contain areas of low as well as high intensity fire, usually in a complex mosaic (Van Wagner 1983). These variable fire intensities result in a heterogeneous pattern of burn severities (effects of fire on the ecosystem) as well as islands of unburned vegetation. The influence of burn severity on plant reestablishment following fire is well documented (e.g. Ahlgren & Ahlgren 1960; Lyon & Stickney 1976; Rowe 1983; Viereck 1983; Ryan & Noste 1985), and the importance of the effects of limited burns and low-intensity fires on the vegetation mosaic has also been recognized (Habeck & Mutch 1973; Rowe & Scotter 1973). However, the spatial heterogeneity of burn severities in the landscape has not been studied explicitly. In this paper, we examine the consequences of the large-scale fires that occurred in YNP during 1988 for landscape structure and heterogeneity of the subalpine plateaus.

The question of how fires affect the heterogeneity of a landscape is complicated by the fact that spatial heterogeneity exists at different scales. For example, there is a pattern of burned and unburned patches across an entire landscape, and there is a heterogeneity of burn severities within a burned patch. One might expect fires to increase landscape heterogeneity by fragmenting continuous blocks of older forest and by introducing younger successional stages to the landscape mosaic, and this appeared to be the case with nearly all fires that were observed in Yellowstone prior to 1988. In 1988, however, fires in some areas were so extensive and so severe that the burned landscape actually appeared less heterogeneous than the mosaic of forest age classes that had been present before the fires. Therefore, we hypothesize that post-fire landscape heterogeneity is a function of the size of fire-created patches. In this paper, we use maps of burn severity within YNP derived from remotely sensed data to address three main objectives. First, we examine the spatial pattern of stand-replacing fire to quantify the isolation of burned areas from unburned or lightly burned areas. Second, we compare the heterogeneity that resulted from fires under moderate and severe burning conditions. Third, we examine the heterogeneity of fire-created patterns on a daily basis and ask whether heterogeneity is related to fire size and the meteorological conditions present at the time of burning.

We hypothesize that the heterogeneity of smaller burned areas will be high and that the heterogeneity of large burned areas will be low. This might occur if fires burning at smaller scales are responsive to several controlling environmental variables, including fuel moisture, fuel type, atmospheric humidity, wind, temperature, and topography. Smaller patches then would be very complex and irregular in shape and have a mixture of burn severity classes. In contrast, large fires might exhibit low heterogeneity if fires burning at these scales are controlled by fewer environmental variables. Very large fires may be controlled mainly by wind velocity and direction and would be less responsive to subtle variation in fuels, moisture, and even topography. If so, these fires would be more uniformly severe and have more rectilinear shapes with a large proportion of the patch being severely burned.

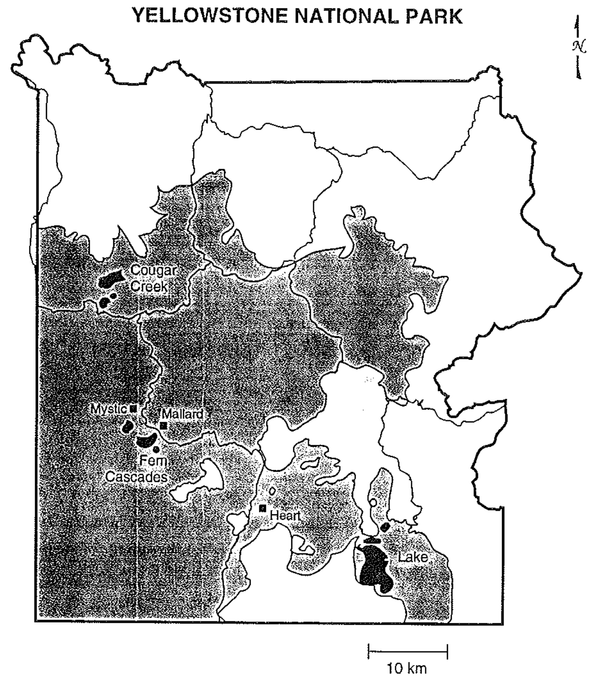

Fig. 1. Map of Yellowstone National Park, Wyoming showing the boundaries of the subalpine plateau (shaded) and the locations of the 12 study areas (shown in black) from which field measurements of burn severity were obtained. Park roads are also indicated.

Background on the Yellowstone fires of 1988

Yellowstone National Park encompasses 9000 km^2 in the northwest corner of Wyoming and is primarily a high, forested plateau. Ca. 80 % of the Park is covered with coniferous forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*). We have chosen to focus just on these subalpine forested plateaus that cover most of Yellowstone and support similar vegetation throughout. Fire has long been an important component of this landscape, and, as in most other parts of the Rocky Mountains, fire has profoundly influenced the fauna, flora, and ecological processes of the Yellowstone area (Habeck & Mutch 1973; Houston 1973; Loope & Gruell 1973; Taylor 1973; Wright & Heinselman 1973; Wright 1974; Arno 1980; Romme 1982; Romme & Knight 1981, 1982; Knight 1987; Romme & Despain 1989; Despain 1991).

A natural fire program was initiated in Yellowstone in 1972 and expanded in 1976 (Anon. 1975), permitting lightning-caused fires to burn without interference under specified conditions. There were 235 such fires observed in the Park between 1972 and 1987. Most of these fires went out by themselves before burning more than a hectare, and the largest fire (in 1981) burned about 3100 ha (D. Despain pers. comm.). The summer weather was usually too wet for fires to spread over large areas. When summer conditions were dry, fire spread was largely constrained by the spatial pattern of forest successional stages on the landscape: fires burned readily in late successional forests, but often died down when they reached early or middle successional stands (Despain & Sellers 1977; Despain 1991).

Given this previous experience with fire, the enormous extent and severity of the 1988 fires surprised many managers and researchers. These fires burned over 250 000 ha in Yellowstone and surrounding lands and were by far the largest fires in the Yellowstone region since the Park was established in 1872 (Despain et al. 1989). Moreover, fires in 1988 spread rapidly through all forest successional stages and appeared to be influenced more by wind speed and direction than by subtle patterns in fuels or topography.

Why were the fires so large? The major reason appears to be the unusually severe weather conditions – characterized by prolonged drought and wind – that existed in 1988, coupled with the fact that the Yellowstone landscape was covered by extensive and, in many places, continuous forests (Romme & Despain 1989). Reconstructions of fire history suggest that the last time

Table 1. Classes of burn severity used to define heterogeneity within the extensive burned areas.

Class	Burn severity	Description
0	Unburned	No sign of fire effects.
1	Light surface burn	Canopy trees still have green needles, although stems may be scorched; soil organic layer still largely intact, though burned in small patches.
2	Severe surface burn	Heavier surface burn; needles on canopy trees were not consumed but are dead; pre-fire soil organic layer largely consumed, but soil covered by dead leaves fallen from the canopy after the fire.
3	Crown fire	Needles of canopy trees completely consumed by fire; soil organic layer almost entirely consumed, and soil is bare with no litter.

a fire of this magnitude occurred in Yellowstone was in the early 1700s. The fires of 1988 may represent a major disturbance event that occurs at intervals of 100 to 300 yr in this landscape (Romme & Despain 1989).

Methods

Field classification of burn severity

Burn severity was characterized in the field in 12 study areas established across the subalpine plateau (Fig. 1). Three study areas were 1 km × 1 km grids of 100 regularly spaced sampling points separated by 100 m (i.e. a 10 × 10 grid of points) and were established in 1989. The remaining nine study areas were irregularly shaped patches ranging in size from 1 to 3600 ha which were established in 1990. Sampling points in these nine patches were arrayed along transects running perpendicularly through the patch in the subcardinal compass directions (NE, NW, SW, SE). Distances between sampling points were determined by the heterogeneity of the burn and ranged between 20 and 100 m. The total number of sampling points was 895.

Field sampling of burn severity was conducted during July and August of 1989 and 1990. At each sampling point, the severity of the burn within a 50-m^2 circular plot centered on the sampling point was recorded. Four visually distinguishable burn severity classes were used (Table 1). Evidence of scorch damage was visible during both years, and dead needles remained on tree branches in moderate burns through 1990. A key distinction among the burn severity classes is that the canopy trees were not killed by the light surface burn. In the severe surface and crown fire classes, however, the canopy trees were killed, and the fire resulted in the stand being replaced. We distinguish further between the two severities of stand-replacing fires because the severe surface fire and crown fire may differentially affect plant re-establishment. The dominant tree, lodgepole pine, is serotinous, and therefore its seed bank is in the canopy. A severe surface burn does not consume the canopy, thereby leaving the seed bank intact, whereas a crown fire can severely reduce or eliminate the seedbank. Post-fire tree seedling densities in YNP appear to be a function of burn severity (Anderson & Romme 1991; Tinker et al. in press).

Interpretation of remote imagery

We obtained a full (185 km × 185 km) LANDSAT 4 Thematic Mapper (TM) scene (Scene ID Y42574-17403x0) centered on the Park and taken on 2 August 1989. The entire scene was cloud-free. This image, taken one season after the fires in late summer, was ideal, since the needles of scorched trees in moderate burns had turned brown by this time but had not yet dropped off. The scene was georectified by using road intersections and other prominent visible features from existing basemaps obtained from the YNP Geographic Information System (GIS) Laboratory. Georectification was done within the Geographic Resources Analysis Support System (GRASS) (Anon. 1991) using a total of 22 control points distributed across the entire Greater Yellowstone Ecosystem. The overall root mean square error upon rectification was < 27.20 m.

Classification of the image was done only for the subalpine plateau, eliminating the lower elevation sagebrush-grasslands and extreme mountainous terrain. A shaded map of the subalpine plateau then was developed to eliminate classification problems resulting from differential illumination. The sun angle (54°) and sun azimuth (131° east of north) were used with a digital elevation model obtained from the YNP GIS Laboratory to produce a raster shaded relief map following the technique of Horn (1981). This shaded map duplicated the illumination conditions when the scene was made. We divided the image into brightly – and nominally – illuminated portions and performed a separate classification on each portion. A frequency histogram of the 100 illumination categories generated for the shaded relief layer indicated a normal distribution of illumination. Because the mode of the distribution was at category 81, we used this threshold to divide the scene. The two resultant maps were recombined later to produce the final product.

Our field observations of burn severity were used as training sites for image classification. Only points recorded as being wholly within a single burn class (not on

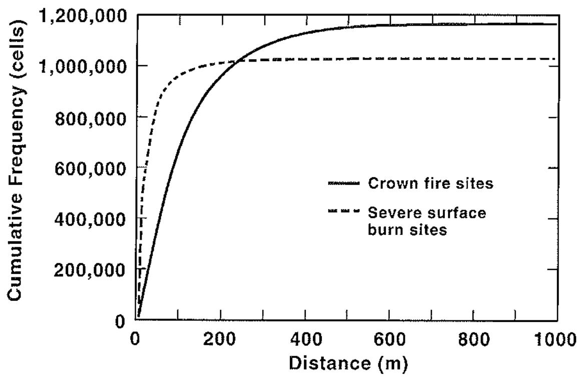

Fig. 2. Cumulative frequency distribution of the distance of grid cells of moderate and crown fire burn to the nearest unburned or lightly burned cell (i.e. green edge).

an edge between classes) were used as training sites, for a total of 642. The positions of ground points had been recorded on 7.5 minute topographic maps in the field, and we estimated their locations by using (1) triangulation; (2) existing base maps of elevation, roads, and rivers; (3) low-altitude aerial photos; and (4) our field notes. We believe that the locations of these points are known to within ±15 m in most cases. Polygons which were known to have had no fires in 1988 (rivers and roads were avoided) also were delineated to improve discrimination of the unburned category, and these polygons were added to the training layer. A total of 742 981 unburned, 64 light surface burn, 94 severe surface burn, and 329 crown-fire sites were included in the final training map.

A spectral signature using all seven bands of the TM scene was developed for each burn severity category by using the GRASS 4.1 program *i.gensig*. Spectral signatures for each category in each band file were normally-distributed (i.e. Gaussian in nature). These signatures were used in a maximum-likelihood discriminant analysis classification using the GRASS 4.0 program *i.maxlik*. The resultant map (Fig. 4) was in agreement with the ground experience of experts, and the map compared well with a previously-existing NPS map (Despain et al. 1989), although the categories differed. The spatial resolution of the final burn severity map was 30 m × 30 m. Comparison of the interpreted severity classes on the map with our ground observations indicated that the percent of cells classified correctly was: unburned, 96.4 %; light-surface burn, 64.1 %; severe-surface burn, 62.8 %; and crown fire, 80.2 %.

The maximum-likelihood classification produced more light surface burn than expected, and some of these cells were not associated spatially with severe surface or crown-fire burns. We expected that the greatest uncertainty in our classification would be associated with light surface burns, which are difficult to detect remotely because there is little effect on the canopy. In addition, this class had the smallest number of training sites. It is possible that the maximum-likelihood classification was responding to some other phenomenon (e.g. mountain pine beetle damage or the remnants of previous fires), but this is not clear. We decided that the presence of these isolated light surface burn cells would not adversely affect our analyses of heterogeneity within the perimeters of the burned areas.

Analyses of landscape heterogeneity

Isolation of areas of stand-replacing burn

The size of the 1988 fires led to the impression that there were very extensive burned areas that might be quite a distance from unburned forest, which could provide sources for plant propagules or cover for animals. We used distance to the nearest 'green edge' to estimate the degree of isolation of areas of stand-replacing fire across the entire subalpine plateau. Using GRASS, distance maps were created for areas of severe surface and crown fire burn in which each cell in the distance map recorded the shortest distance between that cell and the nearest green edge. A green edge was defined as an unburned or lightly burned cell (burn severity classes 0 or 1), because light surface burn sites retained their canopies and regained their pre-fire herbaceous vegetative cover within 2 yr (Turner et al. unpubl. data). Cumulative frequency distributions were then plotted as a function of distance to the nearest green edge to determine the relative degree of isolation of burned areas.

Comparing 'early' and 'late' fires

The 1988 fire season in Yellowstone initially appeared similar to other dry years observed in the Park, but burning conditions became extreme as the summer progressed. By late summer, thousand-hour fuel moisture was less than 10 % (Renkin & Despain 1992), indicating extremely dry conditions. We compared areas that burned early and late during the 1988 fire season to analyze the heterogeneity that resulted from moderate and extreme burning conditions. Maps of daily burn perimeters were obtained from USDA Forest Service's Intermountain Fire Research Laboratory (Rothermel et al. 1994). Early fires were defined as those that burned between June 1 and July 31, and late fires were defined as those that burned between August 20 and September 15 (Fig. 3). Landscape heterogeneity in the early and late maps was analyzed by using SPAN (Turner &

Ruscher 1988; Turner 1990a, 1990b) and computing the following parameters: total area burned; percent of area burned in each burn severity class; indices of dominance and contagion (O'Neill 1988; Turner 1990a); and edge-to-area ratio.

We hypothesized that the spatial scale of the pattern of burn severities might vary between the early and late fires. To examine potential scale-dependent differences in spatial pattern, we compared 18 paired sub-sections of early and late fires. Sliding 100×100 grid-cell windows ($6.25\ km^2$) were moved across the burned map, and the proportions of the window that burned during the early and late intervals were tabulated. The window was considered to represent early fires if at least 50 % of the burned area within the window resulted from fires occurring between June 1 and July 31. Similarly, if at least 50 % of the burned area resulted from fires occurring between August 20 and September 15, the window was considered to represent late fires. For early fires ($n = 18$ windows), the proportion of the area affected by fire, p, ranged from 0.345 to 0.780. Because landscape pattern is affected by p (e.g. Gardner et al. 1987), each sub-section of early fire was paired with a late fire having a similar value of p. We then computed the frequency distribution of fire patches, the size of the largest patch, the amount of edge and lacunarity indices (Plotnick et al. 1993) for each of the 36 sub-sections of the burned landscape.

Lacunarity is a multi-scaled method for determining the texture associated with patterns of spatial dispersion calculated by the gliding box algorithm described by Plotnick et al. (1993). Windows of a given size 'glide' across the map; at each window position, the number of cells occupied by the habitat of interest (e.g. crown fire) is recorded, producing a frequency distribution of habitat counts for that window size. The lacunarity for that box size is computed by taking the ratio between the first moment of the distribution and the squared second moment of the distribution. The process is repeated with successively larger boxes, providing a series of lacunarity values at successively larger scales. Low values for the lacunarity index indicate geometric objects that are homogeneous (i.e. random), while high values indicate objects with a wide range of gap sizes (i.e. a clumped pattern). As a neutral model (Gardner et al. 1987) for scale-dependent pattern, we also generated a random map for each value of p used in the early and late comparison. Analysis of variance was used to test for significant effects in lacunarity, size of the largest burned patch, and the amount of edge between burned and unburned habitat as a function of the map type (early fire, late fire, or random) and the scale at which pattern was measured (100, 200, 400 and 800 m).

Heterogeneity as a function of fire size

The definition of 'fire size' is problematic because continuous burned patches often represent fires that burned over many days and under many burning conditions. On some days, the fire burned only a few hectares; on other days, thousands of hectares were burned. Therefore, we used the total area burned per day as mapped by Rothermel et al. (1994) as an index of fire size. Area burned per day reflects the suite of burning conditions (e.g. wind speed, wind direction, fuel moisture) that influenced fire behavior and hence size. We hypothesize that the resulting patterns of heterogeneity within burned areas are related to fire size and controlled by the severity of the burning conditions.

Several approaches were used to analyze the spatial patterns of burn severity as a function of fire size. First, we used GRASS to calculate the area of each burn severity class contained within the daily burn perimeter identified by Rothermel et al. (1994) and computed a dominance index (O'Neill et al. 1988; Turner 1990) with the proportions of the landscape within each burn class. The proportions and the dominance index were then plotted against total area burned per day, and regression analysis was used to determine the strength of the relationship between pattern and fire size.

Daily fire spread maps also were used to explore weather conditions as potential influences on patch heterogeneity. First, stepwise multiple regression was done in SAS to explore the relationship between the total area burned per day and the following daily weather-related parameters obtained for the Old Faithful area: 1000-hr time-lag fuel moisture (TLFM); 100-hr TLFM; 10-hr TLFM; 1-hr TLFM; mean relative humidity; maximum relative humidity; minimum relative humidity; maximum temperature; minimum temperature; wind speed; and total precipitation. Next, we used stepwise multiple regression to examine the relationship between the proportion of total daily burned area in each burn class and dominance as a function of daily burned area and the same weather parameters listed above. In all analyses, a log transform was used on the area burned per day.

Results

Isolation of areas of stand-replacing burn

Across the subalpine plateau study area, a total of 229 465 ha were included within the perimeter of the burn (as defined by Rothermel et al. 1994). Of that area, 28 % was unburned, 16 % was lightly burned, 25 % had moderate burn severity, and 31 % was crown fire (Fig. 4).

More than 75 % of the moderate burn sites were

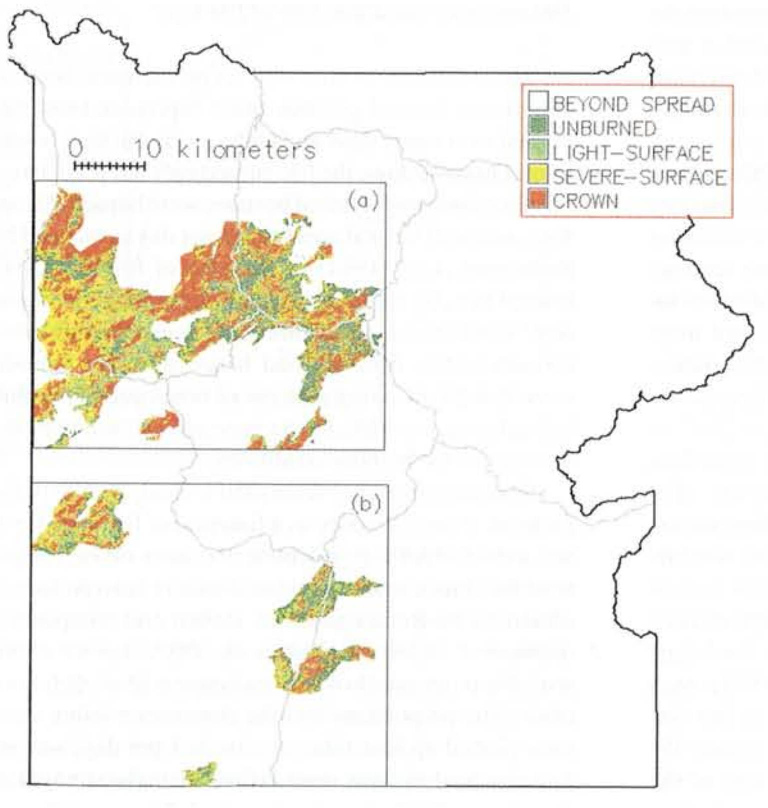

Fig. 3. Map of burn severity for sections of Yellowstone National Park where fires burned (a) between June 1 and July 30, 1988 (early fires) and (b) between August 20 and September 15, 1988 (late fires).

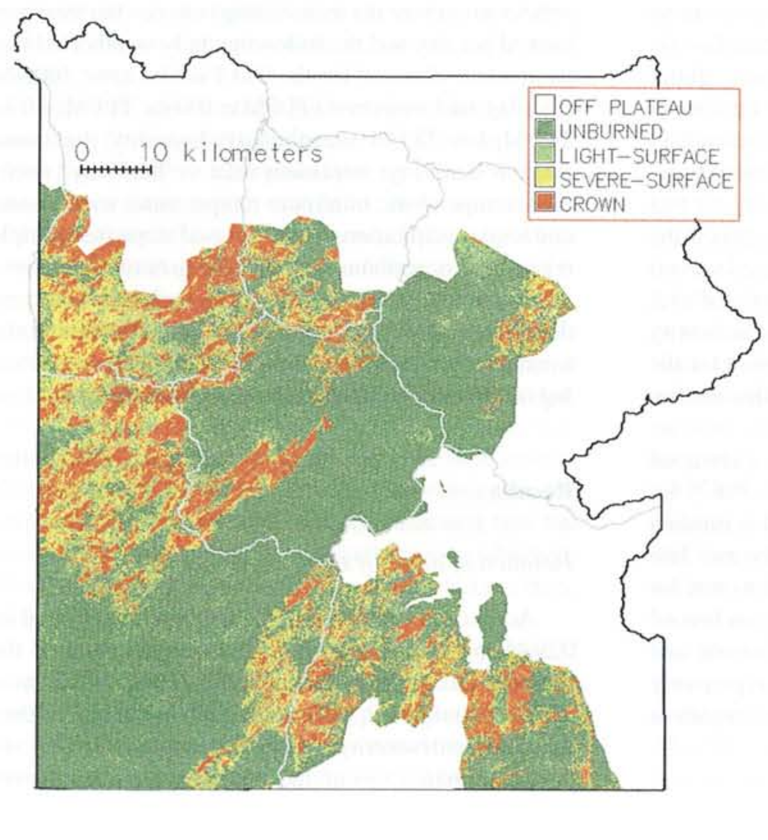

Fig. 4. Map of burn severity on the subalpine plateau of Yellowstone National Park as interpreted from a Landsat Thematic Mapper scene taken on August 2, 1989.

Table 2. Results of analyses of the spatial pattern of burn severities for the area on the subalpine plateau that burned early (June 1 to July 31) and late (August 20 to September 15) during the 1988 fire season in Yellowstone National Park (see Fig. 3). Dates of burning were obtained from Rothermel et al. (1992). Analyses were conducted using SPAN (Turner 1990).

Attribute		Early fires		Late fires
Total area within burn perimeter (ha)		19 555		157 726
Proportion, p, in each burn severity class:				
Unburned		0.293		0.282
Light surface burn		0.189		0.145
Severe surface burn		0.266		0.244
Crown fire		0.251		0.328
Dominance index		0.009		0.028
Contagion index		0.266		0.303
Total no. of edges between burn classes		60 343 (3017 km)		412 069 (20 603 km)
Edge:area ratio (km:ha)		0.154		0.131
No. and mean size (cells) of patches[a]	*No.*	*Mean size*	*No.*	*Mean size*
Unburned	1472	15.6	10 119	17.6
Light surface burn	4801	3.1	31 256	2.9
Severe surface burn	4499	4.6	30 046	5.1
Crown fire	1449	13.6	9720	21.3

[a]Patches were defined by identifying contiguous cells of the same type in the four cardinal directions.

within ~40 m of a green edge (i.e. unburned or light surface burn), and all were within 200 m of a green edge (Fig. 2). Of the crown fire sites, 50 % were within 50 m from a green edge and 75 % were within 200 m of a green edge; very few crown-fire sites were > 500 m from a green edge. However, given the spatial extent of the crown fire areas, the cumulative frequency distribution indicates that nearly 16 000 ha of crown fire sites were > 200 m from a green edge.

Comparing 'early' and 'late' fires

The late fires were approximately eight times larger than the early fires (Table 2, Fig. 3). Late fires were characterized by a greater proportion of the area in crown fire and a lower proportion of the area in light surface burn as compared to the early fires (Table 2). Dominance was very low for both the early and late fire maps, indicating a relatively even distribution of burn severity classes, but there was a three-fold increase in dominance in the late fires. Contagion also increased in the late fires as compared to the early fires (Table 2), indicating an increase in the degree of clumping in the pattern. Although total edge increased in the late fires as area burned increased, the edge:area ratio was slightly lower in the later fires when compared to the early fires. The number of individual patches in different burn severity classes was greater in the late fires than in the early fires, but mean patch size showed the greatest increase for crown fire sites (Table 2). The mean size of crown fire patches was 13.6 cells in the early fires but increased to 21.3 cells in the late fires. The mean size of light and severe surface burn patches showed little change between early and late fires.

The analysis of variance of scale dependent changes in texture, as measured by the lacunarity index, is shown in Table 3. The proportion of the area burned by crown fires, p, is a continuous variable with 1 df, scale was evaluated at 100 m, 200 m, 400 m, and 800 m with 3 df and treatment was either a random map or maps of early and late fires, resulting in 2 df. Although the effect of p, scale, and treatment are all significant, an orthogonal partitioning of the treatment sum of squares (Anon. 1992) shows that difference exists only between random and actual fires ($F = 1491.9, P < 0.0001$) and not between the early and late fires ($F = 0.03, P > 0.85$). Similarily, an analysis of variance of differences between the 18 early and 18 late fire subsections, corrected for differences in p, showed no significant differences in the number, size, or amount of edge produced by the fires.

Table 3. Analysis of variance for the measurement of lacunarity at three spatial scales (100, 200, 400 and 800 m) in three different classes of 100 × 100 grid cell maps (early fires, late fires and random) containing the same proportion of the landscape affected by fire. Model $r^2 = 0.68$.

Source	DF	Mean square	*F* value	*Pr* > *F*
P	1	1.0798	133.12	0.0001
Scale	3	0.5118	63.07	0.0001
Treatment	2	6.0578	747.47	0.0001
Error	857	0.0082		

Heterogeneity as a function of fire size

The area burned per day varied through the 1988 fire season, with the largest burns occurring during the late summer (Fig. 5). The percentage of burned area in each burn severity class also varied with fire size. Large burns tended to have greater percentages of crown fire (Fig. 6a) and smaller percentages of light surface burns (Fig. 6c). However, small to intermediate sized burns exhibit relatively high variability in the percentages of the area in each burn class (Fig. 6). When these values are combined into a dominance index, we see a a trend toward decreasing dominance with increasing burn size, indicating that larger burns have a slightly lower tendency to be dominated by a single burn class than do smaller burns (Fig. 7). This probably reflects the relatively high proportion of severe surface burn present in fires of small size (Fig. 6b).

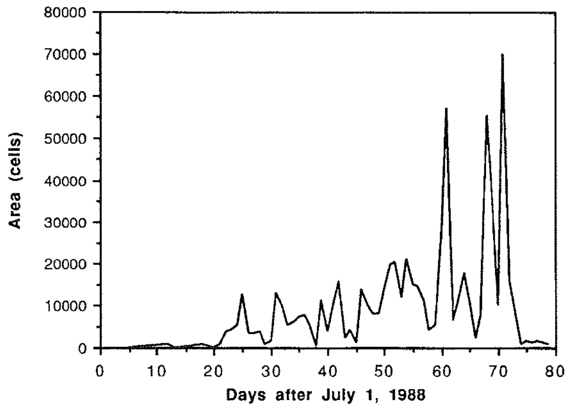

Fig. 5. Area burned per day across the subalpine plateau in Yellowstone National Park during the 1988 fire season (data obtained from Rothermel et al. 1992).

Table 4. Results from stepwise multiple regression analysis of the daily percentage of burned area within each burn severity class and dominance index as a function of total area burned per day and several weather-related parameters obtained from the Old Faithful area.

Variable	Partial r^2	P	Coefficient
Log (Daily area burned)			
100-hr Time-Lag Fuel Moisture	0.265	0.0001	12.302
1000-hr TLFM	0.133	0.0031	41.282
Maximum relative humidity	0.088	0.0021	3.971
Model total	0.486		
Light Surface Burn			
Log(daily area burned)	0.168	0.0008	3.871
10-hr TLFM	0.078	0.0145	– 0.136
Maximum temperature	0.033	0.1021	– 0.678
Model total	0.279		
Moderate Burn			
Log(daily area burned)	0.320	0.0001	6.696
Minimum relative humidity	0.029	0.1038	2.173
1-hr TLFM	0.030	0.0955	1.427
Model total	0.379		
Crown fire			
Log(daily area burned)	0.423	0.0001	9.834
10-hr TLFM	0.054	0.0147	5.293
Model total	0.477		
Dominance Index			
Log(daily area burned)	0.230	0.0001	4.793
100-hr TLFM	0.077	0.0115	0.298
Model total	0.307		

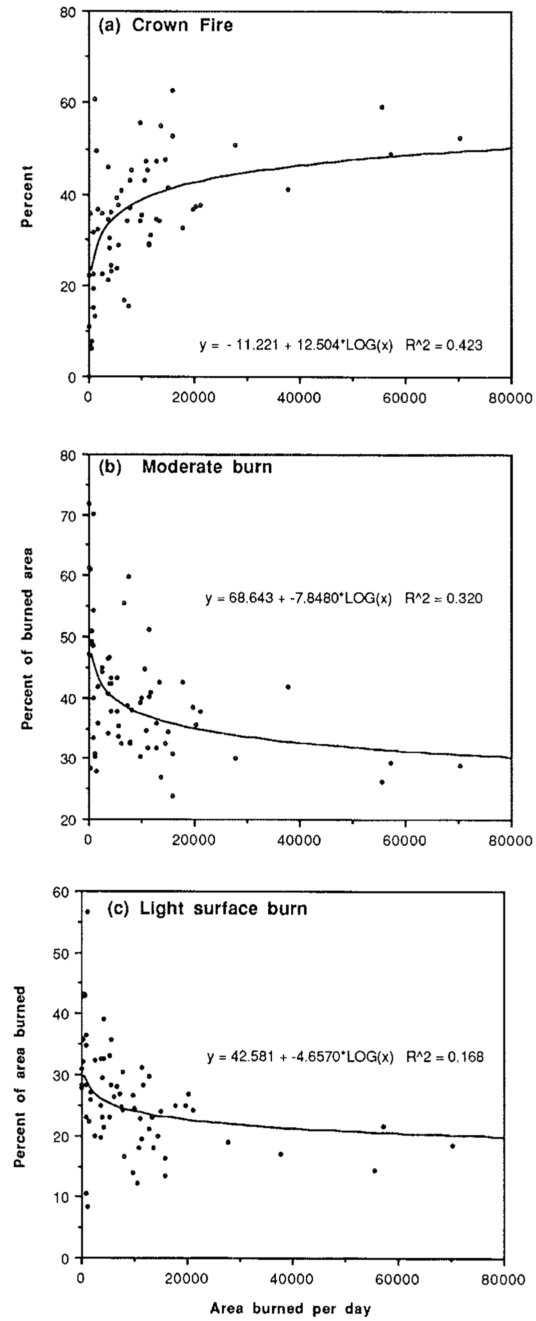

Fig. 6. Percentage of the area within daily burn perimeters in (a) crown fire, (b) moderate burn, and (c) light surface burn as a function of daily fire size for fires that occurred on the subalpine plateau of Yellowstone National Park during 1988.

Variation in total area burned per day was explained primarily by hundred-hr and thousand-hr fuel moisture (Table 4). Maximum relative humidity also was a significant factor in the regression. These three variables explained nearly half the variance in daily burned area.

The proportions in each burn severity class and the dominance index were influenced by the total area burned; one-hr, ten-hr and hundred-hr fuel moisture; maximum temperature; and minimum relative humidity (Table 4). The daily area burned always explained the greatest variance when compared to the other significant variables. The stepwise regression models explained from 28 to 48 % of the variance in the dependent variables.

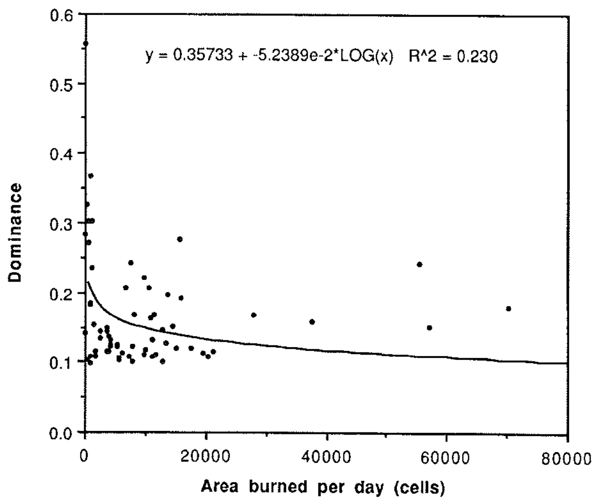

Fig. 7. Dominance index as a function of daily fire size for fires that occurred on the subalpine plateau of Yellowstone National Park during 1988.

Discussion

The spatial mosaic of burn severities is important for plant mortality and reestablishment following crown fires. Extensive areas that experienced fires of high severity are likely to have few resprouting individuals, and may even have had much of the seedbank (in both the soil and canopy) destroyed. Many forest herbs, for example, resprout vigorously from surviving roots and rhizomes in lightly burned areas but must reestablish from seed in severely burned patches. Remnant unburned or lightly burned patches within a severely burned area can provide a seed source that might considerably increase the rate of plant reestablishment.

The spatial heterogeneity of burn severity patterns is also likely to influence a variety of other ecological processes. For example, the amount of edge between mature and early successional forest that is created by an extensive crown fire will vary with burn patterns – a patchy distribution of severely burned areas and lightly burned or unburned stands is likely to increase the browse available for wild ungulate populations (Christensen et al. 1989). Landscape-level burn patterns will also affect watershed dynamics (Minshall et al. 1989) because the removal of vegetation by fire alters the relative amounts of water lost through evapotranspiration, surface flow, and subsurface flow (Knight et al. 1985). For a given proportion of burned area, a high degree of patchiness in burn severity may ameliorate the effects of fire on streamflow and water quality (Knight & Wallace 1989).

Isolation of areas of stand-replacing burn

The generally close proximity of severely burned areas to unburned or lightly burned areas (Fig. 4) was somewhat surprising, because the visual impression of Yellowstone after the fires was of immense patches of severely burned forests stretching for many kilometers. However, the major fire 'runs' in 1988, in which thousands of hectares burned in a single day, generally were long and narrow in shape, such that even the most extensive patches of crown fire were lined by less severely burned and unburned forests. Moreover, at least some small patches of less severely burned forest were present in all of the large crown fire patches.

This finding has important implications for regeneration of the burned forests. Few severely burned sites were very far from a less severely burned site that could potentially serve as a source of propagules for regeneration. Other studies (Anderson & Romme 1991; Turner et al. unpublished data) have shown that survival of shrubs and herbs increased along the fire severity gradient from crown fire (lowest survival) to severe surface fire to light surface fire. These fire survivors flowered profusely in 1990 - 1992. The major seed bank for lodgepole pine is in the canopy, and seed survival was greater in areas of surface fire than of crown fire.

The effective dispersal distance varies among species, of course, such that there is no single distance from an unburned or lightly burned edge that constitutes 'isolation' of a crown fire site from a seed source. The silvicultural literature (Fowells 1965) suggests that lodgepole pine can naturally restock clearcuts up to 60 m from the uncut forest edge. This would imply that roughly 30 % of the crown fire area and 75 % of the severe surface burned area lies within a seed shadow of living lodgepole pine (Fig. 4). Many of the major herbaceous species, e.g. fireweed (*Epilobium angustifolium*) and hawkweed (*Hieracium albiflorum*), have plumed, wind-dispersed seeds that may be carried great distances by the wind (Solbreck & Andersson 1987). Thus, there probably are no areas out of reach of wind-dispersed seeds. However, distances from seed sources to the center of large patches of crown fire may be too great for effective dispersal of species having heavy, round seeds – e.g. lupine (*Lupinus argenteus*) – or specialized dispersal mechanisms (e.g. involving animals or other factors). We are currently conducting other studies to evaluate the specific effects of fire size and severity on reestablishment of plant species having various modes of reproduction.

Comparing 'early' and 'late' fires

The primary difference between fires that burned early and late during the 1988 fire season was the total area burned and the proportion of the burn in the crown fire severity class. Indices of pattern obtained by analysis of the entire early and late landscapes (Fig. 3) suggest a slight increase in the degree of spatial aggregation of crown-fire burns in the late fires as compared to the early fires (Table 2). However, once we control for the proportion, p, of the landscape burned and the spatial extent of the analysis, differences in spatial patterning between early and late fires cannot be detected. Thus, while late fires may generally burn faster and hotter, it is not possible to distinguish differences in texture (e.g. lacunarity indices) or pattern (e.g. measures of edges, patch size, etc.) at any spatial scale after the fires have occurred. This suggests that the effect of large fires on biota is most likely through the amount of resource affected (area burned) rather than through scale-dependent changes in pattern.

Heterogeneity as a function of fire size

One of the interesting implications of the analysis of heterogeneity as a function of area burned (Fig. 6) is that large fires are far more predictable than small fires in terms of the landscape mosaic that they create. For example, when daily fire spread was less than about 20 000 cells (1250 ha), the proportion of the burned area that was crown fire varied widely, from 5 - 60 %, but when the burned area exceeded 20 000 cells, the proportion of crown fire consistently fell within the narrower range of 35 - 55 % (Fig. 6a). The proportions of severe and light surface burns showed similar patterns (Fig. 6b, c). Thus, when small fires occur in this system, we cannot predict the relative mix of fire severity classes, but with very large fires we can expect that roughly 50 % will be crown fire, 30 % severe surface fire, and 20 % light surface fire (Fig. 6).

The importance of hundred-hr and thousand-hr fuel moisture in explaining the variation in total area burned per day is consistent with the findings of Renkin & Despain (1992) who reported that extensive fires occurred in YNP between 1972 and 1988 only when 1000-hr fuel moisture was below 13 %. Our results further indicate that total area burned per day is the most important variable explaining the daily percentage of the burned area within each burn severity class; other weather-related variables have minimal explanatory power (Table 4).

Are big fires qualitatively different from small fires?

A central question that arose after the Yellowstone fires in 1988 was whether these fires were merely larger than the fires observed earlier in this century (i.e. a quantitative difference only), or whether they exhibited some new properties and processes that emerge only after crossing some threshold in size (i.e. a qualitative difference). We can begin to address this question by comparing the areas burned early in 1988 to those areas burned later (Table 2). The early fires burned a relatively small area, comparable to the previous big fire seasons of 1931 and 1981, whereas the late fires were far larger than any in this century.

Our results suggest that there were indeed some qualitative differences between the early and late fires. Most striking was the greater proportion of the burn in the crown fire class and lesser proportions of the milder severity classes (Table 2). The larger fires of late summer were generally less heterogeneous than the smaller fires, as reflected in the dominance index, contagion index, and edge:area ratio (Table 2). Interestingly, the average patch size for unburned, lightly surface burned, and severely surface burned areas was about the same for the early and late fires (Table 2). However, the average size of crown fire patches was 50 % greater in the later fires. Because the centers of these large patches may be remote from surviving seed sources for at least some species (as discussed above), recolonization by the species that were present before the fire probably is slower in large patches than in small patches of crown fire. This means that the establishment of opportunistic or invader species may be more likely in the large patches, and thus the successional dynamics following very large fires may be more complex and less predictable when compared to small fires. We have other research in progress to clarify the patterns of early succession in burned patches of varying size.

Implications

The 1988 fires in Yellowstone National Park provided a unique opportunity to address the interactions between pattern and process at large scales. Interactions between disturbance severity and extent, propagule dispersal, species establishment, and local extinction affect the coexistence of species in the landscape. Climatically-induced shifts in disturbance regimes could have important implications for landscape heterogeneity and hence species distributions and abundances (Graham et al. 1990; Romme & Turner 1991). Past climatic changes of small magnitude have caused significant changes in fire regimes (e.g. Clark 1988; Swetnam & Betancourt 1990). Our analyses demonstrate that the pattern of burn severities across the landscape is related to fire size, suggesting that changes in the fire regime could dramatically change the YNP landscape.

The significance of the 1988 Yellowstone fires extends beyond a single national park or research site.

Many other large national parks and wilderness areas in western and northern North America are covered by large expanses of coniferous forest, and they have a similar history of large, severe fires at long intervals (Heinselman 1973; Hemstrom & Franklin 1982; Turner & Romme 1993). Research on the causes and consequences of the Yellowstone fires will provide insight into the patterns and processes expected in other forested landscapes and should broaden our knowledge of the implications of spatial heterogeneity for ecological processes.

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